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Research

Honeybee navigation: following routes using polarized-light cues

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While it is generally accepted that honeybees (*Apis mellifera*) are capable of using the pattern of polarized light in the sky to navigate to a food source, there is little or no direct behavioural evidence that they actually do so. We have examined whether bees can be trained to find their way through a maze composed of four interconnected tunnels, by using directional information provided by polarized light illumination from the ceilings of the tunnels. The results show that bees can learn this task, thus demonstrating directly, and for the first time, that bees are indeed capable of using the polarized-light information in the sky as a compass to steer their way to a food source.

Keywords: honeybee; navigation; polarization vision; orientation

1. INTRODUCTION

Over the past five decades, considerable effort has been devoted to understanding the strategies and visual cues that honeybees (*Apis mellifera*) use to navigate to food sources, and to uncovering the underlying mechanisms [1]. It is well known that the Sun is used as a reference in the bee's internal compass [1,2]. However, when the Sun is obscured by a cloud, it is believed that bees are still able to obtain a compass reference from the unoccluded part of the sky, by making use of the pattern of polarization that the Sun creates in the sky, through Rayleigh scattering of sunlight by the atmosphere [1,3–5].

There is abundant evidence to support the notion that bees have the capacity to sense the direction of the e-vectors in the celestial polarization pattern [6–10]. The photoreceptors in the dorsal region of the honeybee's compound eyes exhibit a strong sensitivity to polarized light [5,11,12]. Moreover, there are interneurons in the medullae of crickets and locusts that exhibit strong polarizational sensitivity [13–17], suggesting that the pattern of polarized light in the sky is indeed analysed by the brain—and such interneurons are likely to exist in the honeybee as well, although this is yet to be demonstrated. However, these observations do not, on their own, demonstrate that bees perceive the polarization pattern of the sky and use it to measure or set their flight course. The requisite proof must come from a behavioural experiment.

To the best of our knowledge, there is no study so far that has examined whether flying bees use information based purely on the e-vector pattern of the sky, to navigate to food sources. This is not surprising, given the technical difficulties of creating and presenting artificially polarized celestial patterns to freely flying, foraging bees.

2. MATERIAL AND METHODS

(a) *General experimental set-up*

The experiments were conducted in a purpose-built all-weather indoor bee flight facility at the University of Queensland. Climate control ensured a temperature of 24°C during the day and 17°C at night. The transparent walls and ceiling of the facility enabled near-daylight illumination, which included the near-UV (300–400 nm).

Individually marked honeybees, originating from a small beehive housed inside the facility, were trained to forage from a four-armed maze, whose entrance was located 4 m from the hive. The maze was composed of four tunnels arranged in the form of a cross, connected to a central 'decision' chamber (figure 1). Bees were trained to enter one of the tunnels, termed the entrance tunnel, which led to the decision chamber. Here, the bees had to choose one of three exit tunnels, according to the polarization of their overhead illuminations, as described later below. The decision chamber itself was

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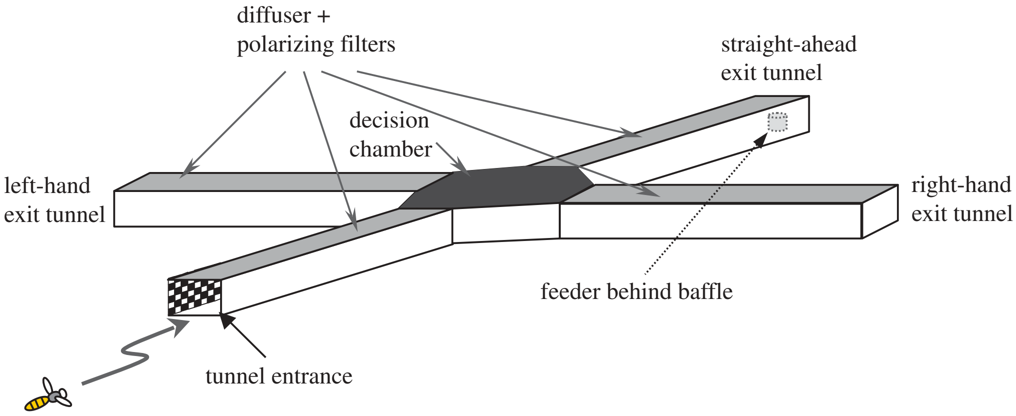

Figure 1. Schematic illustration of the four-tunnel maze used in the study.

lined with back cardboard on the walls, floor and ceiling, and carried no visible internal landmarks. If a bee chose the correct exit tunnel, it received a food reward from a sugar water feeder placed at the end of that tunnel. After feeding, it was released by opening a flap in the tunnel's ceiling, immediately above the feeder. If a bee chose an incorrect tunnel, it received no reward, and was released by opening a similar flap at the end of that tunnel.

Each tunnel was 125 cm long, 11 cm wide and 18 cm high. The walls were lined with a black-and-white checkerboard pattern (check size 2.5 × 2.5 cm) to provide optic flow cues for the bees as they flew in the tunnels. The patterns were printed on paper using a laser printer, and were laminated to facilitate regular cleaning to prevent the bees from using any olfactory cues for navigation through the maze. The floor was lined with white paper, which was frequently replaced for the same reason. The narrow width of the tunnels greatly increased the magnitude of the optic flow that was experienced by the bees, compared with flight in a natural outdoor environment [18,19]. Thus, flight through the maze simulated for the bees an outdoor flight that was approximately 30 times longer [19].

The ceiling of each tunnel provided polarized-light illumination throughout its length. This illumination was created by placing UV-transmitting polarization filter sheets (HN22 linearly polarizing filter, Polaroid) on the ceiling, under a sheet of UV-transmitting diffuser paper that initially depolarized the incident light and provided spatially homogeneous illumination that was devoid of any locally bright spots on the ceiling that the bees could have used as a solar compass.

The polarization of the overhead illumination was either parallel to the axis of the tunnel ('axial polarization') or perpendicular to it ('transverse polarization'). The four tunnels provided different combinations of axially polarized or transversely polarized illumination, depending upon the experiment (as described later below). The bees had to learn to fly to the decision chamber through the entrance tunnel, and then choose an exit tunnel in which the illumination was polarized in the same direction (relative to the tunnel) as in the entrance tunnel. Thus, if the entrance tunnel presented axially polarized illumination, they had to learn to choose an exit tunnel that presented axially polarized illumination; and similarly for transversely polarized illumination.

(b) *Experiments*

Two training and testing experiments were conducted, each using a fresh group of bees. Between 30 and 50 individually marked bees participated in each experiment.

In *experiment 1*, the entrance tunnel presented axially polarized illumination. During the training phase, the 'straight-ahead' exit tunnel presented axially polarized illumination, while the exit tunnels to the left and to the right presented transversely polarized illumination (figure 2*a*). In the tests, the configuration was as in the training (test 1), or with the axially polarized illumination presented in the left-hand exit tunnel (test 2) or in the right-hand exit tunnel (test 3).

In *experiment 2*, the entrance tunnel presented transversely polarized illumination. During the training phase, the right-hand exit tunnel presented transversely polarized illumination, while the left-hand and straight-ahead exit tunnels presented axially polarized illumination (figure 2*b*). In the tests, the configuration was as in the training (test 1), or with the transversely polarized illumination presented in the straight-ahead exit tunnel (test 2) or in the left-hand exit tunnel (test 3).

During the training phase of each experiment, a feeder was placed at the far end of the 'correct' exit tunnel (i.e. the tunnel that presented illumination that was polarized in the same direction as in the entrance tunnel). The feeder was placed behind a baffle (not shown in figure 1), so that it could not be viewed by the bees from the decision chamber. The other exit tunnels also carried baffles of identical appearance at their ends, so that bees could not learn to choose the correct exit tunnel on the basis of the feeder's visibility.

In the tests, the feeder was removed, the overhead flap at the end of each exit tunnel was opened and a video camera was placed above the end of each exit tunnel to record the arrival of individually marked bees. Bees were admitted into the maze one at a time by opening a flap at the front of the entrance tunnel. Each bee was admitted only after the previous bee had flown through the maze, made its decision and exited the apparatus. This procedure ensured that there was only one bee in the maze at any time during the tests, so that there was no interaction

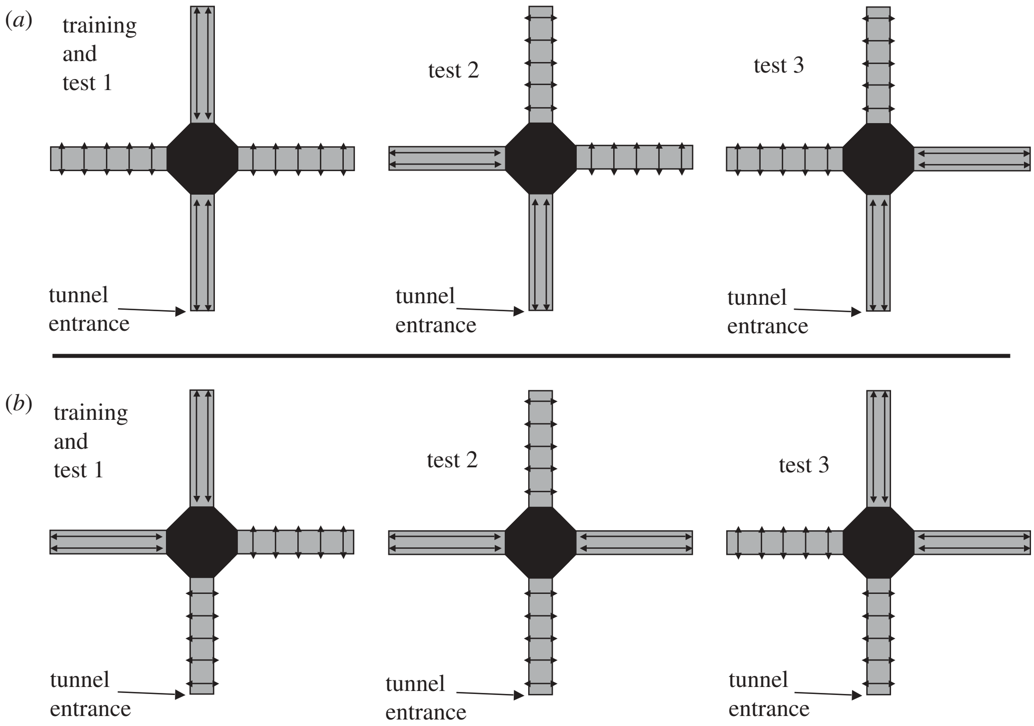

Figure 2. Illustration of the training and test configurations used in (*a*) experiment 1 and (*b*) experiment 2.

between the bees' choices. Prior to each test, the patterns lining the tunnel walls were cleaned and the paper lining the floors was replaced, to prevent the use any olfactory cues in navigation.

For each experiment, training was carried out for two days (6 h per day), during which each bee made *ca* 50 rewarded visits, on average. Tests were then commenced. Each type of test (test 1, test 2 and test 3) was carried out three times, in random order, to obtain sufficient data. Training was continued for 1.5 h between successive tests.

(c) *Data analysis*

The choices made by the trained bees in each test were analysed as follows. First, the choice probabilities were evaluated separately for each individual bee. Thus, for example, if a particular bee had chosen the left-hand, straight-ahead and right-hand tunnels a total of N1, N2 and N3 times over all of the tests of a particular type (say, test 1) during the course of an experiment, the probabilities associated with its choice of the three tunnels in test 1 were calculated as $100 \times (N1/(N1 + N2 + N3))$, $100 \times (N2/(N1 + N2 + N3))$ and $100 \times (N3/(N1 + N2 + N3))$, respectively. The results for the individual bees were then pooled and averaged to obtain the choice probability for each exit tunnel, averaged across all of the bees. This method has the advantages that (i) the performances of all bees are weighted equally, and (ii) the data for the different bees are statistically independent of one another. The two-sample, one-tailed *t*-test for unequal variances (heteroscedastic *t*-test) [20] was used to determine whether any two measured choice probabilities were significantly different from each other. The one-sample, one-tailed *t*-test [20] was used to determine whether any measured choice probability was significantly different from the random-choice level of 33 per cent, which would have been obtained if the bees had chosen randomly among the three exit tunnels.

3. RESULTS

(a) *Experiment 1*

In this experiment, bees were trained to enter a tunnel that presented axially polarized illumination and to choose the exit tunnel that was oriented in the straight-ahead direction, which also presented axially polarized illumination. When the trained bees were tested on the training configuration (test 1), they chose the correct tunnel with a probability of 67 per cent (figure 3*a*). This choice probability is significantly greater than the random-choice level of 33 per cent ($p < 0.0005$), indicating that the bees had learnt this task well, at least with respect to the training configuration. The two other arms of the maze (left-hand tunnel and right-hand tunnel), both of which presented transversely polarized illumination, were chosen with low, and approximately equal probabilities of 15 and 18 per cent, respectively (figure 3*a*). When the trained bees were tested with the axially polarized illumination in the left-hand exit tunnel (test 2), they continued to show a preference for the straight-ahead tunnel, although the preference for it was now reduced to 51 per cent, and this choice probability was still significantly greater than the random-choice level of 33 per cent ($p < 0.0005$). At the same time, there was an approximate doubling of the preference for the left-hand tunnel, which presented the axially polarized illumination, from 15 per cent in test 1 to 28 per cent in test 2 (figure 3*a*). This increase in preference for the left-hand tunnel was statistically significant ($p < 0.01$). The preference for the right-hand tunnel (which presented transversely polarized illumination)

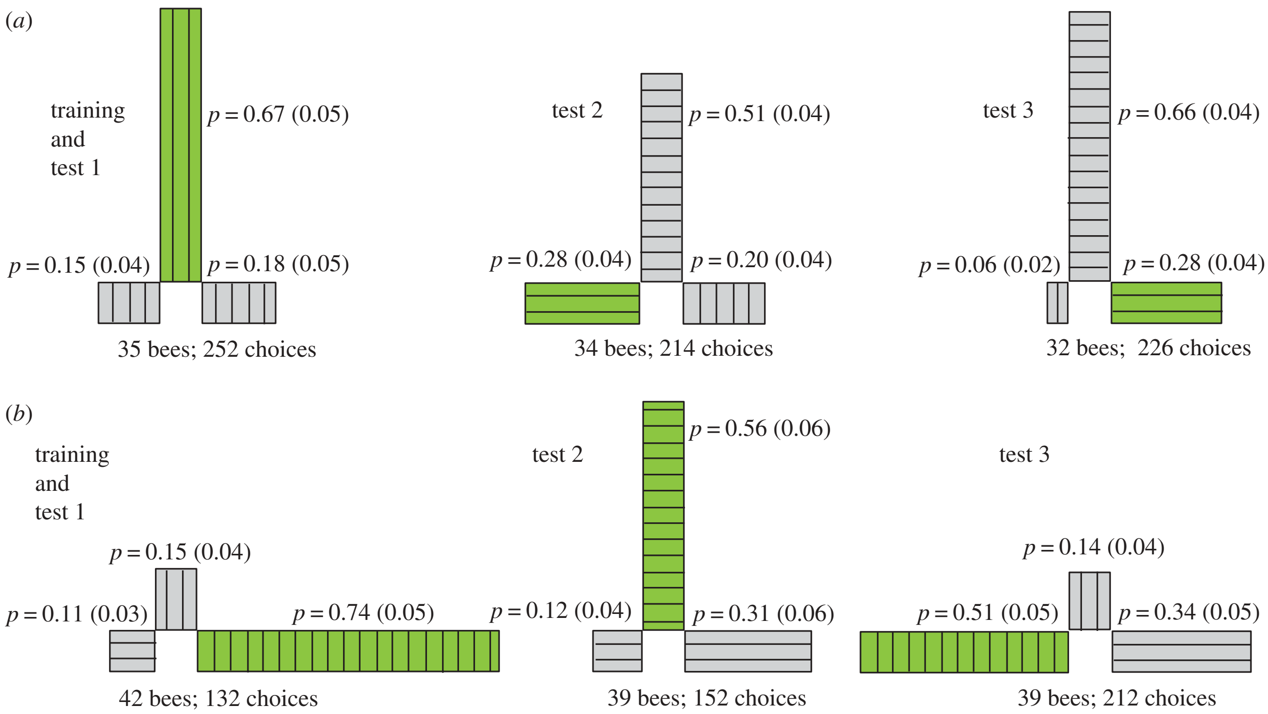

Figure 3. Results of (*a*) experiment 1 and (*b*) experiment 2, showing the mean choice probabilities, and standard errors of the means (in parentheses) for each exit tunnel in tests 1, 2 and 3, evaluated as described in §2. The stripes denote the direction of polarization of the illumination in each tunnel. In each panel, the correct exit tunnel (the tunnel presenting the same illumination as in the entrance tunnel) is shown in green.

remained essentially unaltered (figure 3*a*; $p > 0.35$). When tested with the axially polarized illumination in the right-hand exit tunnel (test 3), the bees again showed the highest preference for the straight-ahead tunnel (66%), and this choice probability was again significantly greater than the random-choice level of 33 per cent ($p < 0.0005$). However, with respect the two remaining tunnels, the bees' preference was now reversed to favour the right-hand exit tunnel, which presented the axially polarized illumination. The preference for this tunnel increased from 18 per cent in test 1 to 28 per cent in test 3 (figure 3*a*). This increase was close to being statistically significant ($p = 0.058$). At the same time, the preference for the left-hand exit tunnel, which presented axial polarization in test 2 and transverse polarization in test 3, decreased from 28 to 6 per cent (figure 3*a*), which was highly significant ($p < 0.00001$, *t*-test).

Very similar results are obtained if the choice probabilities in the various tests are evaluated using a slightly different procedure, namely, pooling the choices made by all of the bees for each tunnel (electronic supplementary material, figure S1*a*).

In summary, experiment 1 reveals that the bees indeed attended to the polarized-light information in the maze, but that their propensity to use this cue to navigate through the maze was overridden by a strong tendency to use a much simpler, geometrical strategy—which was to fly straight ahead through the maze to reach the reward. Very similar results are obtained if the choice probabilities for each tunnel in the various tests are evaluated using a slightly different procedure, namely, pooling the choices made by all of the bees (electronic supplementary material, figure S1*a*).

(b) *Experiment 2*

In this experiment, bees were trained to enter a tunnel that presented transversely polarized illumination and to choose the right-hand exit tunnel, which also presented transversely polarized illumination. When the trained bees were tested on the training configuration (test 1), they chose the correct tunnel with a probability of 74 per cent (figure 3*a*). This choice probability is significantly greater than the random-choice level of 33 per cent ($p < 0.0005$), indicating that the bees had learnt this task well. The two other arms of the maze (left-hand tunnel and straight-ahead tunnel), both of which presented axially polarized illumination, were chosen with low probabilities of 11 and 15 per cent, respectively (figure 3*b*). When the trained bees were tested with the transversely polarized illumination in the straight-ahead exit tunnel (test 2), they showed a clear preference for this tunnel, choosing it with a probability of 56 per cent (figure 3*b*). The preference for the straight-ahead tunnel was significantly greater than the random-choice level of 33 per cent ($p < 0.0005$). The two other exit tunnels, which presented axially polarized illumination, were chosen with significantly lower probabilities (left-hand: 12%; $p < 0.000001$; right-hand: 31%; $p < 0.002$). However, between these two tunnels, the bees showed a clear and statistically significant preference for the right-hand tunnel ($p < 0.004$). When the trained bees were tested with the transversely polarized illumination in the left-hand exit tunnel (test 3), they showed a clear preference for this tunnel, choosing it with a probability of 51 per cent (figure 3*b*). The preference for the left-hand tunnel was significantly greater than the random-choice level of 33 per cent ($p < 0.005$).

Of the other two tunnels, both of which presented axially polarized illumination, the bees showed a clear and statistically significant preference for the right-hand tunnel ($p < 0.002$), which was chosen more than twice as often as the straight-ahead one.

Very similar results are obtained if the choice probabilities in the various tests are evaluated using a slightly different procedure, namely, pooling the choices made by all of the bees for each tunnel (electronic supplementary material, figure S1*b*).

In summary, the results of experiment 2 reveal a clear and strong preference for the bees to always choose the exit tunnel that carries the same pattern of polarized-light illumination as the entrance tunnel. This is true regardless of whether the correct exit tunnel is to the right, to the left or 'straight ahead'. Thus, the trained bees were clearly able to navigate the maze by making use of the polarized-light information that was provided in the tunnels. However, tests 2 and 3 also reveal that the bees displayed a small, but consistent and significant bias in favour of the right-hand tunnel. This indicates that while the bees were relying primarily on polarized-light information to navigate the maze in this experiment, they were also learning a simple geometrical strategy, namely, to 'turn right' at the intersection to reach the goal.

4. DISCUSSION

The ability to use polarized light for navigation has been demonstrated clearly and unequivocally in walking animals such as the desert ant [21] and the dung beetle [22,23]. This has been achieved by showing that the direction of locomotion of a homing desert ant, or of a dung beetle departing with its quarry, can be systematically altered by changing the direction of the e-vector of the overhead illumination. However, this ability has so far not been demonstrated in honeybees—or, indeed, in any other airborne animal—because of the obvious technical difficulties associated with varying the overhead illumination during flight over large distances. The present study has overcome this hurdle, at least for honeybees, by using a narrow tunnel to simulate a long journey, and manipulating the illumination in the tunnel.

Earlier studies have shown that the waggle dances of bees returning from a food source can be systematically altered by illuminating the hive with artificially polarized light and varying the direction of polarization of this illumination (e.g. [1,7,8]). These experiments are telling in that they demonstrate that bees can perceive and react to polarization patterns. However, because these studies were restricted to modifying behaviour within the hive, they do not reveal whether bees flying outdoors to a food source are able to gauge and set their flight direction purely from the pattern of polarization that is present in the sky.

Jacobs-Jessen [24] showed that when foraging bees were captured and released from a hole in the centre of a circular table that was illuminated from above with polarized light, the bees ran towards the periphery of the table in four different preferred directions relative to the e-vector of the illumination. While this experiment clearly demonstrates that bees have the capacity to sense the direction of the e-vector, they do not indicate whether they use this information to measure or set their direction of flight when they fly towards a known food source. In another study, von Frisch [1] arranged for bees to emerge from their hive through an aperture at the centre of a circular table (as above), with a horizontal sheet of glass positioned just above the table. This encouraged the bees to walk, rather than fly, to the periphery of the table before flying out through a specific exit towards an outdoor feeder to which they had been trained. There were exit holes all around the periphery, but only one hole was open—the one that pointed towards the feeder. He found that, when the experiment was carried out under the open sky, the bees learned to walk in the correct direction to find the exit hole. This was true regardless of whether the Sun was visible, or screened off by a mask, allowing only a part of the remaining blue sky to be visible. While this elegant experiment demonstrates that the bees were using celestial cues to gauge and set their walking direction, it does not reveal the nature of the relevant cue—which could have been the position of the Sun, the polarization pattern of the sky, the intensity or spectral gradients in the sky or a combination of all of these cues.

Our experiments demonstrate, for the first time, that foraging bees can read and set the direction of their flight by using information that is based purely on the polarized light pattern of the sky. Experiments 1 and 2 provide evidence that bees flying to a food source are able to set a course to the destination by using polarized-light information from the sky. They also reveal that bees are capable of using additional information, when available, for navigation. For example, cues based on the geometry of the path through the tunnel also seem to play a significant role. Indeed, geometrical cues play a dominant role when the path through the maze is relatively simple, as is the case in experiment 1. However, when the path through the maze is less straightforward (no pun intended), bees evidently place a greater emphasis on other navigational cues, when they are available. This is demonstrated in experiment 2, where the bees' navigation is clearly dominated by the polarized-light cues that are provided by the overhead illumination. Further work, involving navigation through more complex mazes, may be one way to discourage the bees' reliance on geometrical cues and permit a more comprehensive investigation of polarization-based navigation in the laboratory. Another approach to exclude the use of geometrical cues might be to randomize the position of the correct exit tunnel during the training, while providing consistent polarizational information, thus requiring the bees to disregard path geometry and rely solely on polarizational cues. Our experimental paradigm of flying bees through tunnels with polarized overhead illumination should also enable investigation of whether bees rely on their celestial polarization compass not just when flying a straight, direct route to a food source, but also when making detours around a large obstacle such as a hill—which would require different compass bearings to be selected for different legs of the journey.

Finally, it is worth mentioning that the experiments reported here represent the successful culmination of a long series of unsuccessful attempts in our laboratory to investigate orientation based on polarized light in the honeybee. For example, T. Labhart, C. Labhart & M. V. Srinivasan (2005, unpublished experiments) and M. Dacke & M. V. Srinivasan (unpublished experiments) attempted to train bees to distinguish between light sources that presented polarized light of different e-vector orientations in a Y-maze. These experiments were unsuccessful or only marginally successful, regardless of whether the stimuli were presented to the bees frontally, or in their dorsal visual fields. In another study, T. Labhart, C. Labhart & M. V. Srinivasan (2006, unpublished experiments) were again unsuccessful in their attempts to 'steer' bees through a Y-maze by manipulating the orientation of polarized light from an overhead source positioned above the branch point. These unsuccessful experiments underscore the importance of context in eliciting the appropriate behavioural responses in honeybees. It appears that the polarization-analysing system of the honeybee is 'switched on' during flight only when the bee experiences a polarized-light pattern in the dorsal region of its visual field throughout a long (or simulated long) journey. Attempts to train bees to distinguish between different e-vector orientations at the end of their journey (as in a Y-maze) are apparently not successful because the polarization-sensing system is 'switched off' when the bee nears its destination.

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